POPULATION DYNAMICS AND LIFE HISTORY OF *CREPIDULA CONVEXA* SAY (GASTROPODA: PROSOBRANCHIA) IN DELAWARE BAY [1]

GORDON HENDLER AND DAVID R. FRANZ

Rutgers—The State University, New Brunswick, New Jersey and Biological Sciences Group, University of Connecticut, Storrs, Connecticut 06268

Crepidula convexa is a relatively mobile calyptraeid limpet with large eggs, direct development, and a protandric sexuality. It is distributed from New England south to the Gulf of Mexico and the West Indies. We report here on a population in Delaware Bay, New Jersey, studied from June 1966 through September 1968. These findings complement previous observations by W. R. Coe (1936, 1938, 1942a, 1942b, 1949) on the biology of this and other species of *Crepidula*.

Coe (1936, 1942a, 1942b) investigated growth rates, sexual transformation, and development of *Crepidula* species on both coasts of the United States. His observations of *C. convexa* were apparently based primarily on Massachusetts animals (Woods Hole) attached on the shells of *Littorina littorea* or on hermit crab-inhabited gastropod shells. He found that *C. convexa* entered the male sexual phase at 3 weeks of age, when 3–6 mm long. In the next or transitional phase, oogenesis was found to occur before spermatogenesis has been completed but the hermaphroditic condition was too transient to permit self fertilization. He found that mated males entered the transitional phase at 6–8 mm when several months old and that, at least in aquaria, males ordinarily move from female to female. In males isolated from females, however, the male phase ended after only a month, but a longer transitional period ensued. The female phase is attained at about 6 months at lengths ranging from about 6 mm to a maximum of 13 mm.

This report is an extension of Coe's work. It defines the relation between protandric sexuality and the sexual composition of the population, emphasizes the importance of male mobility for phoretic dispersal, and provides further information on the life history of this species.

MATERIALS AND METHODS

Location

The population of *C. convexa* studied lives on a sand flat adjacent to the New Jersey Oyster Research Laboratory near Green Creek, lower Delaware Bay (New Jersey). The habitat consists of a broad, very gently sloping tidal flat that extends bayward from a narrow, marsh-bordered beach. Water temperature varies seasonally from near freezing to 30° C and may fluctuate as much as 5° C during a summer

tidal cycle. Salinity also varies seasonally but usually remains within the range of 20–26‰, although a change of up to 2‰ during a single tidal cycle is not uncommon. In addition to temperature and salinity stresses, epibenthic organisms in this habitat are subjected to dehydration, severe siltation and burial, and winter ice scouring.

Massive quantities of clam shells (*Spisula solidissima*) are distributed near shore each July as cultch (artificial substrate) for metamorphosing oyster larvae. During autumn most cultch and attached oysters are transplanted to deeper waters while the remainder may become assimilated into a small oyster reef. *Crepidula convexa* appears each summer on newly distributed cultch and a portion of the population remains on the reef each autumn and through the winter.

Methods

For almost 2 years monthly collections were made during low tides. Specimens on cultch and others on *Pagurus* (Hermit Crab)-inhabited snail shells were gathered separately. Those not immediately examined were held in running bay-water in the laboratory. Every specimen of *C. convexa* on each piece of substrate was detached and inspected foot-up in a dish of baywater. Sex was determined by the stage of development of the phallus in relation to the body size of the living animals, and shell length was measured with a calibrated stereomicroscope.

C. convexa passes through five recognized sexual phases: immature; phallus-bud; male; transitional; female. Immature animals exhibit only a slight prominence on the right side of the neck, at the site of the developing phallus. Phallus-bud snails possess a small and peglike phallus. Males are animals with a muscular, functional phallus. Transitional phase animals, produced from males and possibly also from phallus-buds, are characterized by a degenerate phallus, small in relation to total body length. Females are the largest animals and frequently retain a diminutive remnant of the phallus.

Results

The intertidal *C. convexa* is primarily found in cultch areas that remain wet during low tide or on *Nassarius obsoletus* shells inhabited by *Pagurus longicarpus*. In the remainder of this report, *Crepidula* on cultch is referred to as "cultch forms" and those on the *Nassarius* shells as "*Pagurus* forms."

Fecundity

The data on the fecundity of Delaware Bay *C. convexa* presented below are based on 250 brooding female-phase snails examined during the summer of 1968.

The egg mass of *C. convexa* is similar in form to that of other Calyptraeidae. Each is composed of a group of egg capsules joined by a sticky pad (Fig. 1). During an incubation period lasting approximately two weeks, the egg mass is held beneath the ventral face of the neck lappets. It may either be cemented to the substrate by the sticky pad or the pad may be attached to the propodium and thus unattached to the substrate.

The egg capsules have a feature not described for other members of the genus. Each is divided into two compartments (Fig. 1) that hold approximately equal numbers of eggs. The capsule is initially folded in half along the axis of the stalk,
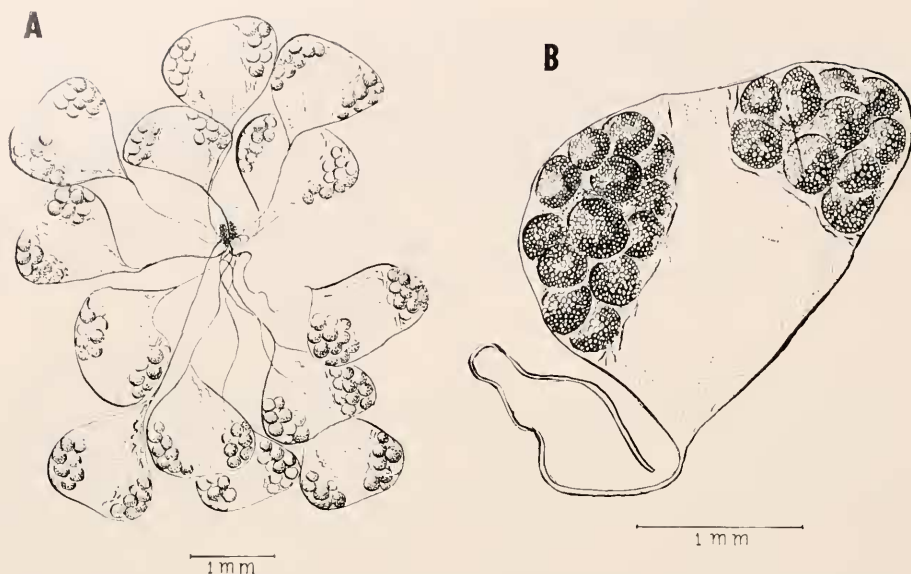
FIGURE 1.   Egg mass and egg capsules of *C. convexa;* (A), an egg mass, consisting of a series of capsules radiating from a sticky tab which may be attached to the substrate; (B), a single capsule showing ova separated into two compartments, drawn from preserved sample flattened under a coverslip.
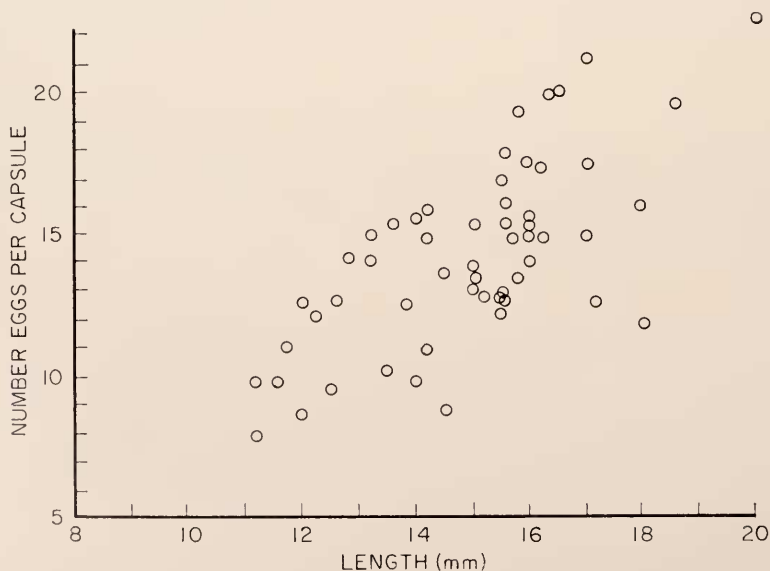

FIGURE 2.   Relationship between shell length and the number of eggs per capsule; cultch form, June, 1968.
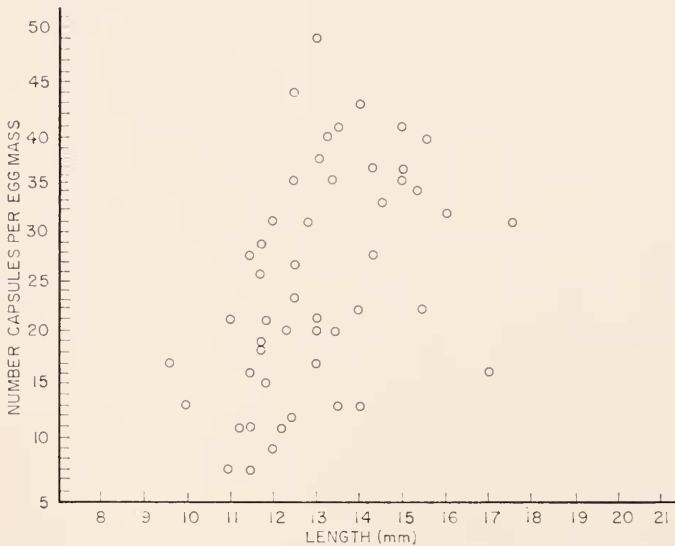
FIGURE 3. Relationship between shell length and the number of egg capsules per egg mass; cultch form, June and July, 1968.

but unfolds to accommodate the growing embryos. The compartment membranes disappear by the time the embryos have developed to a motile stage.

For the purposes of the following discussion, four stages in larval development are recognized: *early gastrula,* including all stages from the zygote to the appearance of external cilia; *trochophore,* for the ciliated motile larva prior to the appearance of the velum; *veliger,* for both shelled and shell-less embryos that possess a velum; and *post-veliger,* for larvae in which the velum is resorbed and the foot is well developed.

Table I shows the occurrence of each of these developmental stages per capsule during June and July, 1968. Each observation represents the average of five capsules from a single egg mass (all of the capsules in a given egg mass are at approximately the same stage of development). These data reveal that there is a significant decline in the numbers of veligers per capsule in relation to trochophores, from an average of about 14 per capsule to 11 per capsule.

The relationship between shell length and both the numbers of eggs per capsule and the number of capsules per egg mass is shown in Figures 2 and 3 (cultch form only). Although the variability is high, it is evident that both of these aspects of fecundity are size-specific, the largest animals producing the greatest numbers of eggs per capsule as well as more capsules per egg mass. These figures also indicate that egg production begins in the size range of 10–11 mm although, infrequently, smaller female-phase snails may oviposit.

Total fecundity expressed as the total number of eggs per mass, and as the total number of surviving veligers and post-veligers, is shown in Figure 4 as a function

TABLE I

Occurrence of various developmental stages per egg capsule
(Data includes both cultch and Pagurus *subpopulations, 1968)*

	No. animals	Mean eggs/ capsule	No. animals	Mean trocho-phores/ capsule	No. animals	Mean veligers/ capsule	No. animals	Mean Post-veligers/ capsule
June	68	13.9	25	14.4	14	11.8	18	9.8
July	25	14.2	4	15.5	17	10.7	28	11.5
$\overline{\overline{X}}$		13.8		14.6		11.2		10.9

$\overline{\overline{X}}$ Eggs $= \overline{\overline{X}}$ Trochophores $> \overline{\overline{X}}$ Veligers $= \overline{\overline{X}}$ Post-Veligers (at $P < 0.05$).

of animal size. Egg production varies from somewhat less than 200 per mass to a maximum in excess of 1300 per mass. However, the numbers of embryos reaching the veliger and post-veliger stages range from less than 100 per mass in small animals to close to 1000 in large females. The reduction in the numbers of embryos which occurs during development (Table I) is therefore a phenomenon which clearly exists over the entire size range of ovipositing females.

It is likely that the abortion and disintegration of the lost embryos provides a nutrient source for the surviving embryos. This form of "embryonic cannibalism" was reported also by Coe (1942a) in *Crepidula onyx*, and by Thorson (1940) in *C. walshi*. Thus, it would seem that the contention of Fretter and Graham (1962, page 404) that this is not a normal occurrence in *Crepidula* is not supported. It seems quite extraordinary to us that a direct-developing species like *C. convexa* would, as a matter of course, uselessly expend energy by incorporating more eggs per capsule than will develop.

The fecundity data represented in Figure 4 above reflects egg production per egg mass. It is probable that two or perhaps even three broods may be produced during a summer. We have observed that animals brooding eggs will produce a second egg mass when the eggs are removed. The maximum percentage of brooding females occurs in June and declines in July. Thus egg production is concentrated in a period of about two months between late May and late July. Since the incubation period requires about two weeks, the average production of about three broods per season is further confirmed.

Table II summarizes the fecundity data for the Delaware Bay population and compares it with information provided by Coe (1949) for a Massachusetts population from Woods Hole. The differences are remarkable. Egg diameter is larger, as is the number of capsules per mass and the total number of eggs per mass in the southern population. These differences may reflect not only the longer growing season in Delaware Bay but also the very productive environment there, conducive to the rapid growth of filter-feeding invertebrates such as *Crassostrea virginica* and *Crepidula*.

Life history

Post-veliger juveniles crawl inside the capsule prior to hatching and may remain in a tight clump under the female for more than a day after hatching. *Crepidula*
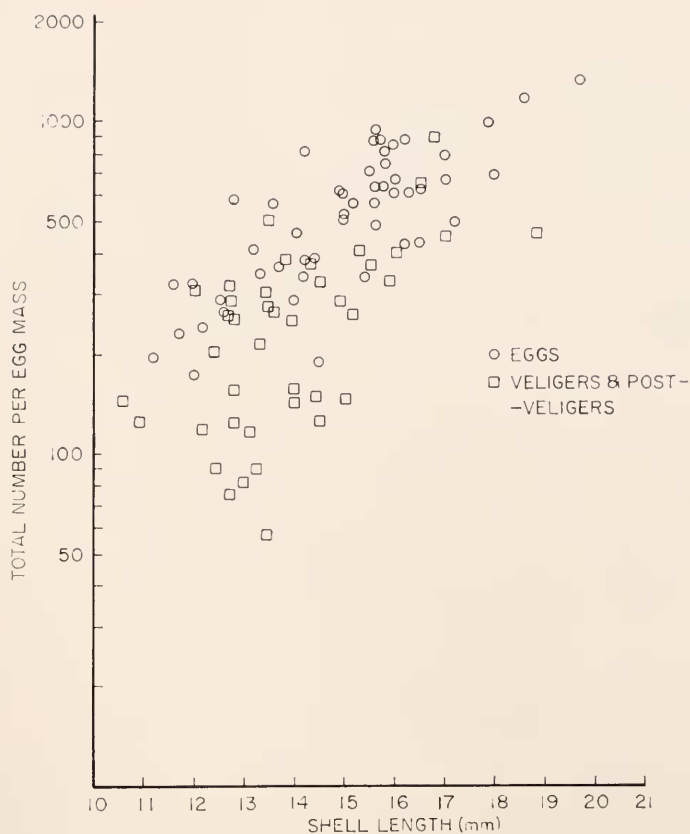
FIGURE 4. Relationship between shell length and: (1) total number of eggs per mass and (2) total numbers of veligers and post-veligers per mass; June and July, 1968.

convexa was not observed to lift its shell and eject its young as does *C. adunca* (Putnam, 1964). In emergent juveniles, 0.95 ± 0.09 mm long, the shell apex is posterior and medial. By the time the shell is 1.5 mm, radial purple stripes appear.

An individual may pass through all sexual phases in its first summer, and size ranges for the successive sexual phases overlap. The immature and phallus-bud stages are respectively 1–8 and 2–9 mm. The males are 1–10 mm, although most individuals with a well-developed phallus are at least 4 mm. The transitional

TABLE II

Fecundity of Crepidula convexa—*Woods Hole and Delaware Bay*

Location	Egg diameter (microns)	No. eggs per capsule	No. capsules per egg mass	Total eggs per egg mass	Reference
Woods Hole	280	8–20	15–25	250 (maximum)	Coe (1949)
Delaware Bay	320*	12*	33*	442*	Present paper

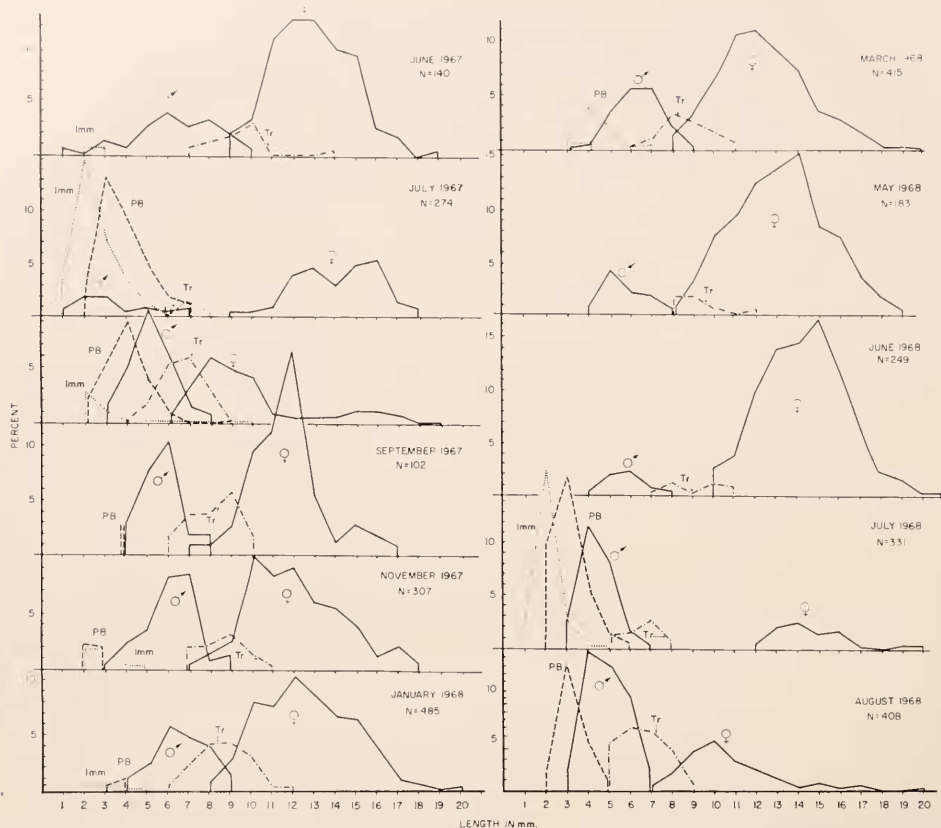* Mean values based on 250 egg masses, summer 1968.

FIGURE 5. Size-frequency histograms for the cultch subpopulation; June 1967–August, 1968.

forms range from 5–14 mm, overlapping both phallus-buds and males.   The existence of transitional forms, with the phallus-length to body-length ratio of phallusbuds and body length of large males, suggests that the male phase may be omitted in nature as well as in experimental isolation.   The females range from 6–20 mm and overlap all other sexual stages in size.   Transition to the female phase can definitely be accomplished in one season, since 7.0 mm females produced eggs during their first summer.   The occurrence of females as large as 20.0 mm suggests a life span of two seasons (1½ years) or more.

Crepidula convexa does not form the permanent chains of mated animals characteristic of some species in the genus.   At any one time, a female carries only one attached male.   If a third individual is attached to the mated pair, it is generally sexually immature.

Data summarizing the sexual composition of the cultch subpopulation are shown in Figure 5; of the Pagurus subpopulation in Figure 6.   Figures and present data on the per cent of females brooding egg masses and of females associated with male-phase animals.

Annual population cycle

Oviposition probably begins in late April or early May coincident with the seasonal increase in water temperature. Eggs were first observed in the field on 12 May, when water temperature had risen to about 15.0° C. At this time, females dominate the population (Fig. 5) and the percentage of brooding females approaches 100 per cent. This percentage declines to about 50 per cent in July, and to 25–30 per cent in August. Factors mediating this decline may be depletion of sperm in the seminal receptables, exhaustion of energy reserves, and an increasing percentage and number of newly transformed females which have not yet been inseminated.

Brooding of the new year class in June results in a large number of immature and phallus-bud individuals in July. These, plus older males, comprise the pop-
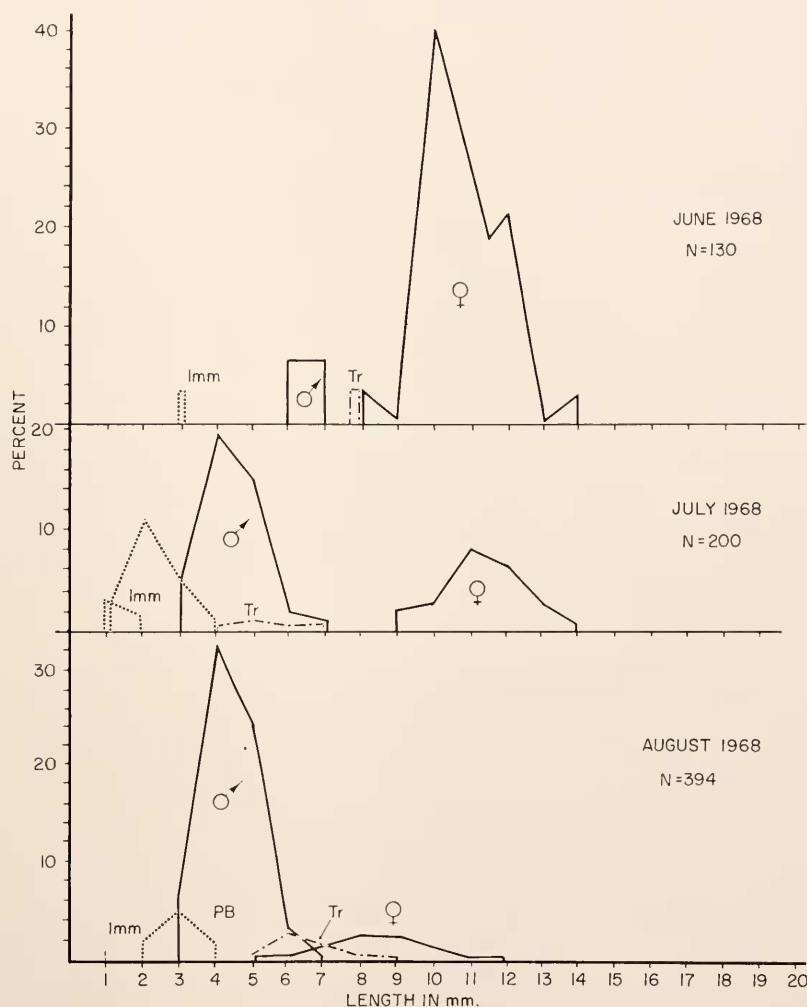

FIGURE 6. Size-frequency histograms for the *Pagurus* subpopulation; June–August, 1968.

ulation components at the left of the July histograms (Fig. 5). The component on
the right consists only of older females.

During August the immatures and phallus-buds which appeared the previous
month transform to males. Consequently, a large component of males is generated
at the left on the August histogram and the number of immatures declines. The
same histograms show a simultaneous increase in female and especially in transi-
tional stages. The flattening at the right end of the histogram, however, indicates
that a large proportion of the females are recently transformed and therefore of
smaller size. These transitions and females have been produced from males of the
previous year, and perhaps to a lesser extent from males of the new year class.

Throughout June, July and August, the number of mated males (males associ-
ated with females in a mating position) increases from less than 10 per cent to
30–40 per cent, in concert with decreasing oviposition. Since the ratio of males to
females is approximately constant for both June and July, the increase in mating at
this time must result from an increased tendency for males to mate. In August, the
influx of recently transformed males further increases mating. By September,
males and females are the two principal sexual components of the population al-
though the young stages present in August remain important. The transitional
phase now encompasses an increased size range, indicating that larger males are
becoming transitional and larger transitional phases becoming females. At the
same time, most of the immatures are transformed to males. This September dis-
tribution pattern is in sharp contrast with the nearly constant ratio of male to
transitional phases in July and August. In September, males are animals spawned
during the summer while females include animals spawned in both the current
and the previous summer.

The percentage of large females increases from September to November.
Growth is also shown by the progressively greater modes of the female and other
phases from November to March. The similarity of the histograms for the winter
months and the accumulation of female phases indicates a slow but significant trans-
formation of sexes during this period. Consequently females (many of them re-
cently transitional unmated) dominate the population in May and the cycle starting
with spring oviposition begins again.

Cultch and Pagurus *subpopulations—The phenomenon of dwarfism*

Studies of the dual substrate forms of *Crepidula convexa* (Franz and Hendler,
1969) have shown that the broad, flat shell shape of the cultch form and the narrow,
high shape of the *Pagurus* form is caused by limitations inherent in the available
substrate. Shell growth in *Pagurus* forms is restricted by the length and curvature
of the *Nassarius* shell. Hence large *Pagurus* forms tend to orient on the long axis
of the *Nassarius* shell, with their head at the aperture; they often produce a skirt
of shell which overgrows the sides of the *Nassarius* shell. Because of substrate
restrictions *Pagurus* form females attain a maximum length of only 14.0 mm while
cultch forms of almost 20.0 mm are present throughout the year.

In addition to size and shape, the percentage of females with attached males in
the *Pagurus* subpopulation (up to 80%) exceeds the cultch subpopulation (5–30%).
This probably reflects the lack of space and the isolation of *Pagurus* forms on mov-
ing hermit crabs. The more consistant association of male and female *Pagurus*
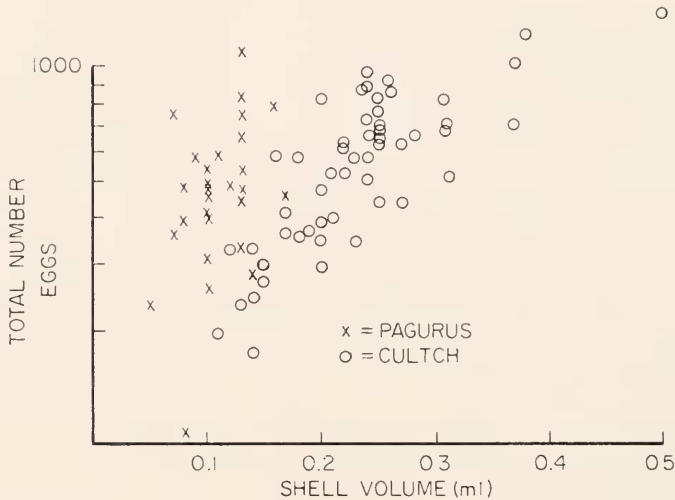
FIGURE 7. Relationship between the total number of eggs per egg mass and the shell volume of *Pagurus* and cultch subpopulations.

forms may account for the longer oviposition period as compared with the cultch forms.

The two substrate subpopulations differ also in their tendencies to attach the egg mass to the substrate. An average of 20 per cent of cultch animals but 70 per cent of the *Pagurus* animals cement egg masses to the substrate rather than clasping them beneath the foot. These differences between the subpopulations suggest that attachment is affected by some environmental stimulus.

Figure 7 shows an additional contrast between the substrate-controlled subpopulations. Although the maximum shell volumes of cultch and *Pagurus* forms are similar (Franz and Hendler, 1970), the shells of most of the ovipositing *Pagurus* forms are less than 0.15 ml, whereas ovipositing cultch forms generally exceed this volume. As mentioned previously, the fecundity of the cultch forms is a size function, females of greater volume producing more eggs. The relationship between female shell volume and fecundity is less clear for the *Pagurus* forms because a majority of the brooding females are less than 0.15 ml volume, while a large number of brooding cultch females attain at least 0.3 ml. It is noteworthy that the total fecundity range for the two forms is the same, the number of eggs per female varying between roughly 100 and 1000. However, *Pagurus* females produce more eggs than cultch females of equal volume, a difference probably indicating a different degree of sexual maturity at an age when their volumes are similar. In other words, large *Pagurus* forms are almost certainly older than cultch forms of equal volume. A growing *Pagurus* form female transferred to a flat substrate would therefore be expected to produce the same number of eggs as a cultch form of greater volume. It appears then that *Crepidula convexa* living in association with *Pagurus* constitutes a true dwarf population, but without any indications of the neoteny observed by Thorson (1965) for *Capulus* associated with *Turritella*.

Changes in the sexual composition of the *Pagurus* subpopulation analogous to

those in the cultch subpopulation occur during the summer (Fig. 6) but transformations may be more rapid in the *Pagurus* form. Both transitional and juvenile stages are relatively rare, possibly because they exist for only short periods and therefore are not adequately represented in the sample. More rapid transformation may also result in exaggerated percentages of *Pagurus* form females in June as of males in August compared to the cultch form sex ratio at these same times. These differences between the subpopulations could be either a direct effect of the substrate or perhaps the indirect result of the greater amount of mating association among the *Pagurus* animals.

Differences between the substrate forms in morphology, mating behavior, breeding cycle, and maturation rate are attributed, directly or indirectly, to the substrate. The *Pagurus* and cultch form populations are not, however, autonomous. There is an interchange of individuals from different substrates mediated by phoresis on *Pagurus*. This exchange prevents the isolation of the two substrate forms and permits *Pagurus* forms to escape crowded hermit crab shells.

Movement of *Pagurus* forms to cultch is suggested by the appearance of male *C. convexa* on bare, isolated surfaces such as newly deposited cultch mounds. These mature settlers do not grow from juveniles present on the surface, nor are they spawned by females in the vicinity; neither do they move by themselves across sand and mud sediments to the cultch mounds.

The feasibility of phoresis was tested in the laboratory. Within 30 hours, *C. convexa* moved both ways, from *Pagurus* to clean cultch, and from cultch to unoccupied *Pagurus*. The animals that transferred to alternate substrates in both tanks were small (4.4 ± 1.4 mm), and were predominantly immatures, males, and few transitional phases. A similar experiment on the sand flat indicated that phoresis is operative in the field. Thus, *Pagurus* in the vicinity with mobile, young *Crepidula* can serve as vectors in the colonization of virgin substrates.

DISCUSSION

In view of the success of congeneric planktotrophic species such as *Crepidula plana* and *C. fornicata,* the existence of direct development in *C. convexa* is interesting, and raises questions as to its adaptive advantage, and its ecological significance. Direct development is generally thought to be an adaptation to extreme environmental stresses such as occur in estuarine, arctic or deep-sea situations (Thorson, 1950). The advantages conferred by direct development include: decreased larval mortality from predation, independence from a planktonic food source, and ready access to suitable substrate. The chief liabilities are the loss of a larval dispersal mechanism and reduction in numbers of young. Assuming that dispersal is desirable, only organisms with strong inherent mobility would be expected to evolve direct development.

The results of this study on the sexual dynamics of the population shed light on the means by which *C. convexa* has circumvented or neutralized the liabilities noted above. Young animals are highly mobile and adept at phoresis, thus facilitating dispersal in the absence of a delicate veliger larva. Moreover, the high mobility of males permits promiscuity so that males mate with more than one female during the breeding season, thereby increasing the reproductive capacity of the population.

The high mobility of young *C. convexa,* affecting as it does both the capacity for dispersal and reproductive success, accounts for the abilities of the species in colonizing new substrates as well as the expansion of its geographic range as noted by Vokes (1935).

Since direct development in *C. convexa* appears linked to a substitute mechanism for larval dispersal, it is possible that a mating system involving mobile males preceded the evolution of direct development. We do not suggest that this evolutionary sequence is a necessary prerequisite for the evolution of direct development in other *Crepidula* species. We feel, however, that in most cases the evolution of direct development involves a complex of adaptations which may be, but are not necessarily, induced by extreme environmental stress. The ultimate problem is to ascertain the actual conditions that initiated the production of direct development from planktotrophic forms and to determine how the eventual sympatry of these forms has come about.

Additional comparative studies on similar forms with direct and planktotropic development are needed before the progressive stages in the evolution of direct development can be uncovered. An ideal situation for such a study exists on the Pacific coast of the United States where, according to Coe (1949) up to 6 *Crepidula* species may coexist, 3 with planktotrophic larvae, and 3 with direct development.

SUMMARY

1. The reproductive biology and population dynamics of two substrate forms *Crepidula convexa* were investigated. The species is a protandric hemaphrodite with direct development.

2. The egg mass differs from other species in the genus in that the capsules comprising it are compartmentalized in early development. Later, the compartment walls break down and there is a decrease in the number of embryos, suggesting the existence of "embryonic cannibalism." Size-specific fecundity of the Delaware Bay population appears higher than published data for a Woods Hole population.

3. There is rarely more than one male associated with a female and the ratio of males to females is low.

4. Life span is at least two seasons. At the beginning of June, when reproduction is maximal, the population is predominantly female. The resulting influx of juveniles shifts the sexual composition of the population in such a way that males dominate by August. The transformation of these males to females during the winter gradually shifts the sexual composition so that females again predominate by Spring.

5. *Crepidula convexa* living on *Pagurus* form a dwarf population which differs from cultch animals in morphology, mating behavior, breeding cycle and maturation rate. These differences are attributed to limitations of substrate. Exchange of individuals between subpopulations is facilitated by phoresis on hermit crabs.

6. The high mobility of young *C. convexa*, which makes phoresis possible, is considered to be the key factor in the success of this species in the colonization of virgin substrates, thus facilitating dispersal in the absence of a larval stage. The capacity of males to fertilize more than one female is also a function of this mobility and is probably the major factor in maintaining a sex ratio (males < females) which favors maximal reproduction.

LITERATURE CITED

Coe, W. R., 1936. Sexual phases in *Crepidula*. *J. Exp. Zool.*, **72** : 455–477.

Coe, W. R., 1938. Influence of association on the sexual phases of gastropods having protandric consecutive sexuality. *Biol. Bull.*, **75** : 274–285.

Coe, W. R., 1942a. Reproductive organs of the prosobranch mollusk *Crepidula onyx* and their transformation during the change from male to female phase. *J. Morphol.*, **70** : 501–512.

Coe, W. R., 1942b. Influence of natural and experimental conditions in determining shape of shell and rate of growth in gastropods of the genus *Crepidula*. *J. Morphol.*, **71** : 35–47.

Coe, W. R., 1949. Divergent methods in development in morphologically similar species of prosobranch gastropods. *J. Morphol.*, **84** : 383–400.

Franz, D. R., and G. Hendler, 1969. Substrate diversity and the taxonomy of *Crepidula convexa* Say (Gastropoda : Prosobranchia). *Occas. Pap. Univ. Connecticut (Biol.)*, **1** : 281–289.

Fretter, V., and A. Graham, 1962. *British Prosobranch Molluscs*. Ray Society, London, 755 pp.

Putnam, D. A., 1964. The dispersal of young of the commensal gastropod *Crepidula adunca* from its host *Tegula funebralis*. *Veliger*, **6** (Supple.) : 63–66.

Thorson, G., 1940. Studies on the egg masses and larval development of Gastropoda from the Iranian Gulf. *Danish Sci. Invest. Iran*, **2** : 159–238.

Thorson, G., 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.*, **25** : 1–45.

Thorson, G., 1965. A neotenous dwarf-form of *Capulus ungaricus* (L.) (Gastropoda, Prosobranchia) commensalistic on *Turritella communis* Risso. *Ophelia*, **2**(1) : 175–210.

Vokes, H. E., 1935. Rate of migration of *Crepidula convexa* Say. *Nautilus*, **49** : 37–39.